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Balitora dehouensis, a new species of cave-dwelling hillstream loach (Teleostei, Cypriniformes, Balitoridae) from the upper Red River, southwestern China

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Abstract

A new species of cave-dwelling hillstream loach (Balitoridae, Cypriniformes), *Balitora dehouensis* **sp. nov.** is described from a cave in Wenshan Zhuang and Miao Autonomous Prefecture, Yunnan Province, China. *Balitora dehouensis* **sp. nov.** is confirmed to be a distinct species by morphological and phylogenetic analysis based on the mitochondrial cytochrome b (Cyt *b*) gene and cytochrome oxidase subunit 1 (*CO*I) gene as well as the nuclear recombination activating gene 1 (RAG1), interphotoreceptor retinoid binding protein (IRBP), and early growth response protein 2B (EGR2B). *Balitora ludongensis* is confirmed to be the third cave-dwelling member of *Balitora*, after *B. anlongensis* and *B. dehouensis*.

Key Words

Balitora, Balitoridae, Cavefish, morphology, phylogeny

Introduction

Hillstream loaches of the family Balitoridae are small dorsoventrally compressed benthic fishes distributed in torrential streams of Himalayas, Indo-Burma, Sundaland, and southern China (Kottelat 2012; Fricke et al. 2025). This taxon, alongside a few sister taxa (Barbuccidae, Gastromyzontidae, Serpenticobitidae) are characterized by enlarged, horizontally placed pectoral and pelvic fins with multiple simple anterior rays, capable of clinging on to boulders and rocks of fast flowing streams, feeding on algae and aquatic invertebrates (Šlechtová et al. 2007; Lujan and Conway 2015). Balitoridae (Originally Balitorinae) was established by Swanson (1839) as a subfamily of Cobitidae to accommodate *Balitora brucei* Gray, 1830. Despite different opinions regarding the nomenclature

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of this family appeared (Bleeker 1859; Fowler 1905; Sawada 1982; Kottelat 1987), scholars have reached a consensus with Balitoridae as the valid family name after Kottelat's (1988a) revision of *Balitora*.

The elucidation of phyletic relationships among Balitoridae genera has remained an enduring challenge in ichthyological systematics. Chen (1980) divided Balitoridae (referred to as Homalopterinae) into two clades, Sinohomalopterini (*Neohomaloptera*, *Sinohomaloptera*, *Lepturichthys*, *Hemimyzon*, *Sinogastromyzon*) and Homalopterini (*Homaloptera*, *Bhavania*, *Travancoria*, *Balitropsis*, *Balitora*) based on the number of maxillary barbels. Kottelat and Chu (1988) revised Balitoridae (referred to as Homalopterinae), proposed a monophyletic group including *Balitora*, *Sinohomaloptera* (=*Balitora*) *Lepturichthys*, *Sinogastromyzon*, *Hemimyzon*, *Metahomaloptera* and *Jinshaia* based on a peculiar oral morphology they share: arched mouth with both jaws covered by a horny sheath; rostral flap divided into three lobes, the median one usually the largest, between rostral barbels; both lips with one or two rows of papillae; lower lip not interrupted: one or two maxillary barbels at the corner of mouth. Such monophyly is confirmed by subsequent phylogenetic studies (Randall and Page 2015; Sidharthan et al. 2021; Luo et al. 2023). Randall and Page (2015) conducted phylogenetic analysis based on the nuclear recombination activating gene 1 (RAG1) gene, recognizing two monophyletic clades (tribes), namely Balitorini and Homalopteroidini, with the former consisting of nine genera, *Balitora*, *Lepturichthys*, *Sinogastromyzon*, *Hemimyzon*, *Metahomaloptera*, *Jinshaia*, *Balitoropsis*, *Pseudohomaloptera* and *Homaloptera*, covering the entire distribution area of Balitoridae, while the latter with a more restricted distribution, represented by only two genera, *Homalopteroides* and *Homalopterula*. Within Balitorini, two major clades are resolved: a strongly supported clade consisting of *Balitora* as the sister group to *Lepturichthys*, *Sinogastromyzon*, *Hemimyzon*, *Metahomaloptera* and *Jinshaia*; and a weakly-supported clade consisting of *Balitoropsis* as the sister group of (*Homaloptera* + *Pseudohomaloptera*). Moreover, contemporary phylogenetic analyses conducted upon the Balitoridae lineage have revealed persistent uncertainties surrounding the taxonomic validity of multiple constituent genera. Non-monophyly of six genera, namely *Balitora*, *Lepturichthys*, *Sinogastromyzon*, *Hemimyzon*, *Metahomaloptera* and *Jinshaia* have been repeatedly adressed in various studies (Liu et al. 2012a; Kumkar et al. 2016; Keskar et al. 2018; Tao et al. 2019; Shao et al. 2020; Luo et al. 2023). To date, taxonomic status of multiple genera within Balitoridae remain obscure.

Although limestone caves and the subterranean river system they held are rather common in the distribution area of Balitorids (Kottelat 1988b), they are typically epigean species, with only two species, *Cryptotora thamicola* and *Balitora anlongensis* previously recorded as cavefishes (Kottelat 1988b; Luo et al. 2023). During two ichthyological expeditions conducted in October 2023 and November 2024 at a subterranean river flowing into the Lujiang River, a tributary of the Red River in Wenshan Zhuang and Miao Autonomous Prefecture, Yunnan Province, southwestern China, Troglobitic balitorid specimens were collected. Although these specimens resembled troglobitic members of *Balitora* morphologically, they are clearly distinguished from all other *Balitora*. spp by an oblique caudal-fin base. Through comprehensive morphological and phylogenetic analysis, these specimens are confirmed to represent a new species, hereby described as *Balitora dehouensis* sp. nov. In addition, another *Balitora* species, *B. ludongensis* was also collected from a stretch of subterranean river in Nanning City, Guangxi Zhuang Autonomous Region, China, thus raising the number of Balitoridae cavefishes to three.

Four *Balitora* (as *Sinohomaloptera* in original description) species from the Red River in Vietnamese literature, with one, *B. nigrocorpa* from the Vietnamese Lo River (the Lujiang River) and three, *B. haithanhi*, *B. vanlani* and *B. vanlongi* from the Vietnamese Gam River (the Nanli River) (Nguyen 2005) were considered invalid by Kottelat (2012) without providing explanation for such arrangement. Only *B. nigrocorpa* is recorded as synonym of *B. kwangsiensis* by Fricke et al. (2025) in reference to subsequent research on Balitoridae that did not include these species in taxonomic analysis due to unavailability of original data and voucher specimens (Bhoite et al. 2012; Liu et al. 2012b). Given that type specimens of these species are reported lost (Endruweit 2014) and no topotypical specimen was available, all four Vietnamese *Balitora* species were included in the morphological comparison of this research based on the original description.

Materials and methods

Sample Collection

All care and use of experimental animals complied with the relevant laws of the Chinese Laboratory of Animal Welfare and Ethics (GB/T 35892-2018). Specimens were captured with hand nets. All specimens were taken pictures immediately after capture, then euthanized, fixed and subsequently stored in formalin solution. Tissue samples were taken from the fins and preserved in 95% ethanol. A total of 17 specimens of *Balitora dehouensis* sp. nov. were obtained, all type specimens were preserved in 8% formalin and stored at the Kunming Zoological Museum, Kunming Institute of Zoology (KIZ), Chinese Academy of Sciences (n = 5) and personal collection of Mr. Hong-Fu Yang (n = 12). An additional collection of *Balitora elongata* (n = 1), *B. kwangsiensis* (n = 3), *B. ludongensis* (n = 7), *B. nantingensis* (n = 1), *Hemimyzon macropterus* (n = 1), *H. megalopseos* (n = 1), *Jinshaia abbreviata* (n = 1), *J. niulanjiangensis* (n = 1), *Lepturichthys fimbriata* (n = 1), *Metahomaloptera omeiensis* (n = 1), *Sinogastromyzon chapaensis* (n = 1), *S.sichangensis* (n = 1), and *S.szechuanensis* (n = 1) were collected for morphological and molecular comparison. All comparative materials were deposited at KIZ. All voucher codes are listed in Table 1 and sampling sites are illustrated in Fig. 1.

Table 1. Voucher code, sampling localities and accession numbers of all sequences used for molecular analysis.

No.	Family/Species	Locality	Voucher	Cyt*b*	*COI*	RAG1	IRBP	ERG2B
	Gastromyzontidae							
1	*Beaufortia szechuanensis*	Zhaotong, Yunna Province, China	IHB0709025	JN177007	JN177067	JN177061	JN177281	JN177253
	Balitoridae							
2	*Balitora anlongensis*	Anlong County, Qianxinan Buyi and Miao Autonomous Prefecture, Guzihou Province, China	GZNU20230215018	OQ754144	OQ784688	OQ754158	OQ754154	OQ754149
3	*Balitora anlongensis*	Anlong County, Qianxinan Buyi and Miao Autonomous Prefecture, Guzihou Province, China	GZNU20230215020	OQ754143	OQ784689	OQ754157	OQ754152	OQ754148
4	*Balitora brucei*	/	ClFEFGB-Bb-02	MK732324	MK388804	/	/	/
5	*Balitora chipkali*	Karnataka, Ramnagar,India	WILD-15-PIS-230	KU378017	KU378004	/	/	/
6	*Balitora chipkali*	Karnataka, Kamra, Joida, India	BNHS FWF 193	KU378016	KU378003	/	/	/
7	*Balitora dehouensis* sp. nov.	Dehou Town, Wenshan City, Wenshan Zhuang and Miao Autonomous Prefecture, Yunnan Province, China	PXR20241123001	PV973998	PV954918	PV974021	PV974054	PV974090
8	*Balitora dehouensis* sp. nov.	Dehou Town, Wenshan City, Wenshan Zhuang and Miao Autonomous Prefecture, Yunnan Province, China	PXR20241123002	PV973999	PV954919	PV974022	PV974055	PV974089
9	*Balitora dehouensis* sp. nov.	Dehou Town, Wenshan City, Wenshan Zhuang and Miao Autonomous Prefecture, Yunnan Province, China	PXR20241123003	PV973996	PV954920	PV974023	PV974056	PV974088
10	*Balitora dehouensis* sp. nov.	Dehou Town, Wenshan City, Wenshan Zhuang and Miao Autonomous Prefecture, Yunnan Province, China	PXR20241123004	PV973997	PV954921	PV974024	PV974057	PV974087
11	*Balitora elongata*	Mengla County, Xishuangbanna Dai Autonomous Prefecture, Yunnan Province, China	20241223002	PV973989	PV954911	PV974019	PV974046	PV974076
12	*Balitora kwangsiensis*	Hekou Yao Autonomous County, Honghe Hani Autonomous Prefecture, Yunnan Province, China	20250125	PV973993	PV954908	PV974028	PV974051	PV974084
13	*Balitora kwangsiensis*	Jiangcheng Hani and Yi Autonomous County, Puer City, Yunnan Province, China	20241225002	PV973995	PV954909	PV974025	PV974052	PV974086
14	*Balitora kwangsiensis*	Xichou County, Wenshan Zhuang and Miao Autonomous County, Yunnan Province, China	20250101001	PV973994	PV954910	PV974026	PV974050	PV974085
15	*Balitora kwangsiensis*	Yuanjiang, Yunnan Province, China	IHB0805547	JN177005	JN177072	JN177059	JN177276	JN177248
16	*Balitora laticauda*	Karnataka, Shimoga, India	WILD-15-PIS-232	KU378011	KU377998	/	/	/
17	*Balitora laticauda*	Maharashtra, Ajara, India	WILD-14-PIS-070	KU378009	KU377996	/	/	/
18	*Balitora longibarbata*	Luoping County, Qujing City, Yunnan Province, China	314	PV974000	PV954916	PV974030	PV974062	PV974077
19	*Balitora ludongensis*	Jingxi City, Baise City, Guangxi Zhuang Autonomous Region, China	GZNU20230215024	OQ754142	/	/	/	/
20	*Balitora ludongensis*	Jingxi City, Baise City, Guangxi Zhuang Autonomous Region, China	GZNU20230215023	OQ754141	/	/	/	/
21	*Balitora ludongensis*	Longan County, Nanning City, Guangxi Zhuang Autonomous Region, China	20250105001	PV974003	PV954922	PV974035	PV974063	PV974097
22	*Balitora ludongensis*	Longan County, Nanning City, Guangxi Zhuang Autonomous Region, China	20250105002	PV974004	PV954923	PV974037	PV974064	PV974095
23	*Balitora ludongensis*	Longan County, Nanning City, Guangxi Zhuang Autonomous Region, China	20250105003	PV974005	PV954924	PV974036	PV974067	PV974096
24	*Balitora ludongensis*	Longan County, Nanning City, Guangxi Zhuang Autonomous Region, China	20250105004	PV974006	PV954925	PV974038	PV974065	PV974094
25	*Balitora ludongensis*	Longan County, Nanning City, Guangxi Zhuang Autonomous Region, China	20250105005	PV974007	PV954926	PV974039	PV974066	PV974093
26	*Balitora ludongensis*	Daxin County, Chongzuo City, Guangxi Zhuang Autonomous Region, China	20241212001	PV974008	PV954927	PV974033	PV974072	PV974099
27	*Balitora ludongensis*	Daxin County, Chongzuo City, Guangxi Zhuang Autonomous Region, China	20241212002	PV974002	PV954928	PV974034	PV974073	PV974098
28	*Balitora mysorensis*	Karnataka, Hattihole, India	WILD-15-PIS-231	KU378018	KU378005	/	/	/
29	*Balitora nantingensis*	Yongde County, Lincang City, Yunnan Province, China	20250328002	PV973991	PV954913	PV974017	PV974048	PV974101
30	*Balitora yingjiangensis*	Nabang Town, Yingjiang County, Dehong Prefecture, Yunnan Province, China	20241228001	PV973992	PV954914	PV974018	PV974049	PV974100
31	*Balitoropsis ophiolepis*	Way Besai River, Lampung Province, Sumatra	Vial 2006-0588	/	KR052868	KP322540	/	/
32	*Balitoropsis zollingeri*	Tha Di River, Nakhon Si Thammarat Province, Thailand	Vial 2005-0948	/	KR052865	KP322535	/	/
33	*Bhavania australis*	/	20241112001	PV973988	PV954907	PV974016	PV974045	PV974074

No.	Family/Species	Locality	Voucher	Cyt*b*	*COI*	RAG1	IRBP	ERG2B
34	*Ghatsa pillai*	Slient Valley, Kerala, India	/	/	MT919712	/	/	/
35	*Ghatsa santhamparaiensis*	Santhampara, Kerala, India	KUFOS-19-AN-GA-42.1	/	MT216532	/	/	/
36	*Hemimyzon formosanum*	/	cyp903	AY392484	KU943001	/	KP695096	
37	*Hemimyzon macropterus*	Huaning County, Yuxi City, Yunnan Province, China	20250414005	PV974011	PV954915	PV974029	PV974058	PV974083
38	*Hemimyzon megalopseos*	Kaiyuan City, Honghe Hani Autonomous Prefecture, Yunnan Province, China	PXR20231011	PV819089	PV792008	PV974043	PV974068	PV974082
39	*Homaloptera confuzona*	/	CBM: ZF 11705	NC_033955	NC_033955	KP322543	/	/
40	*Homaloptera ocellata*	/	CBM: ZF 12287	NC_033953	NC_033953	KP322539	/	/
41	*Homaloptera ogilviei*	/	/	NC_031635	NC_031635	/	/	/
42	*Homaloptera parclitella*	/	/	NC_031634	NC_031634	EU409610	EU409668	EU409732
43	*Homalopteroides smithi*	/	CBM:ZF 12281	NC_033957	NC_033957	KP322546	/	/
44	*Homalopterula gymnogaster*	/	Vial SN25	/	/	KP322554	/	/
45	*Jinshaia abbreviata*	Shimian County, Ya'an City, Sichuan Province, China	20250413003	PV973990	PV954912	PV974020	PV974047	PV974075
46	*Jinshaia niulanjiangensis*	Deze Township, Zhanyi District, Qujing City, Yunnan Province, China	20241211005	PV974010	PV954930	PV974041	PV974059	PV974092
47	*Lepturichthys dolichopterus*	Jianou, Fujian Province, China	IHB0706070	GU084245	JN177091	JN177029	/	/
48	*Lepturichthys fimbriata*	Dadukou District, Chongqing City, China	20250414004	PV974014	PV954934	PV974044	PV974069	PV974081
49	*Lepturichthys fimbriata*	Jinkou, Hubei Province, China	IHB0803128	GU084229	JN177102	JN177182	JN177272	JN177251
50	*Metahomaloptera omeiensis*	Dadukou District, Chongqing City, China	20250315001	PV974012	PV954932	PV974040	PV974070	PV974079
51	*Neohomaloptera johorensis*	/	CBM:ZF 12286	NC_033952	NC_033952	/	/	/
52	*Pseudohomaloptera leonardi*	/	/	NC 008673	NC 008673	EU711130	FJ197076	AB531164
53	*Sinogastromyzon chapaensis*	Hekou Yao Autonomous County, Honghe Hani Autonomous Prefecture, Yunnan Province, China	20241225006	PV974001	PV954917	PV974027	PV974053	PV974102
54	*Sinogastromyzon sichangensis*	Qingshen County⊠Meishan city, Sichuan Province, China	20250414001	PV974013	PV954933	PV974032	PV974071	PV974078
55	*Sinogastromyzon szechuanensis*	Xinjing District⊠Chengdu city, Sichuan Province, China	20250414002	PV974015	PV954931	PV974040	PV974060	PV974080
56	*Sinogastromyzon wui*	Luzhai County, Liuzhou City, Guangxi Zhuang Autonomous Region, China	20250414003	PV974009	PV954929	PV974031	PV974061	PV974091
57	*Travancoria elongata*	Poringal Power House, Kerala, India	/	OK306991	OK306991	/	/	/

Morphometric data acquiring

Morphological analysis on *Balitora dehouensis* sp.nov. and congeners were conducted through voucher specimens and literature.

Measurements were made point-to-point with digital calipers, and data were recorded to an accuracy of 0.01 mm. Measurements of all specimens examined were made on the left side of specimens whenever possible. Subunits of the head are presented as percentage proportions of head length (% HL). Head length and measurements between landmarks on the body are given as percentage proportions of standard length (% SL). Detailed information of morphometric variables followed Kottelat (1988a, 2001). Given the morphological similarity between *B. dehouensis* and troglobitic species of *Balitora*, type specimens of *B. dehouensis* were primarily compared with available specimens and data of known troglobitic members of *Balitora* as well as their congener possessing two pairs of long maxillary barbels, i.e., *B. anlongensis* Luo, *B. longibarbata* (Chen) and *B. ludongensis* Liu. Additional *B. longibarbata* (1977001182, 1977001304, 1977001303, 1977001310, 1977001311) and *B. ludongensis* (2008008640, 2008008636, 2008008639) collections of KIZ were examined for morphological comparison.

Literature review consisted primarily of original descriptions of species and genera as well as results from important comprehensive studies (Fang 1930; Gray 1830; Zheng 1980; Kottelat 1988a; Kottelat 1988b; Kottelat and Chu 1988; Nguyen 2005; Conway and Mayden 2010; Bhoite et al. 2012; Raghavan et al. 2013; Luo et al. 2023; Lei et al., in press).

DNA extraction, amplification, sequencing, and phylogenetic analysis

Fin tissue for molecular analysis was taken from fresh specimens and preserved in 95% ethanol. Primers used in PCR amplification follow Luo et al. (2023). Five molecular markers, namely the mitochondrial cytochrome b gene (Cyt *b*), cytochrome oxidase subunit 1 gene (*CO*I),

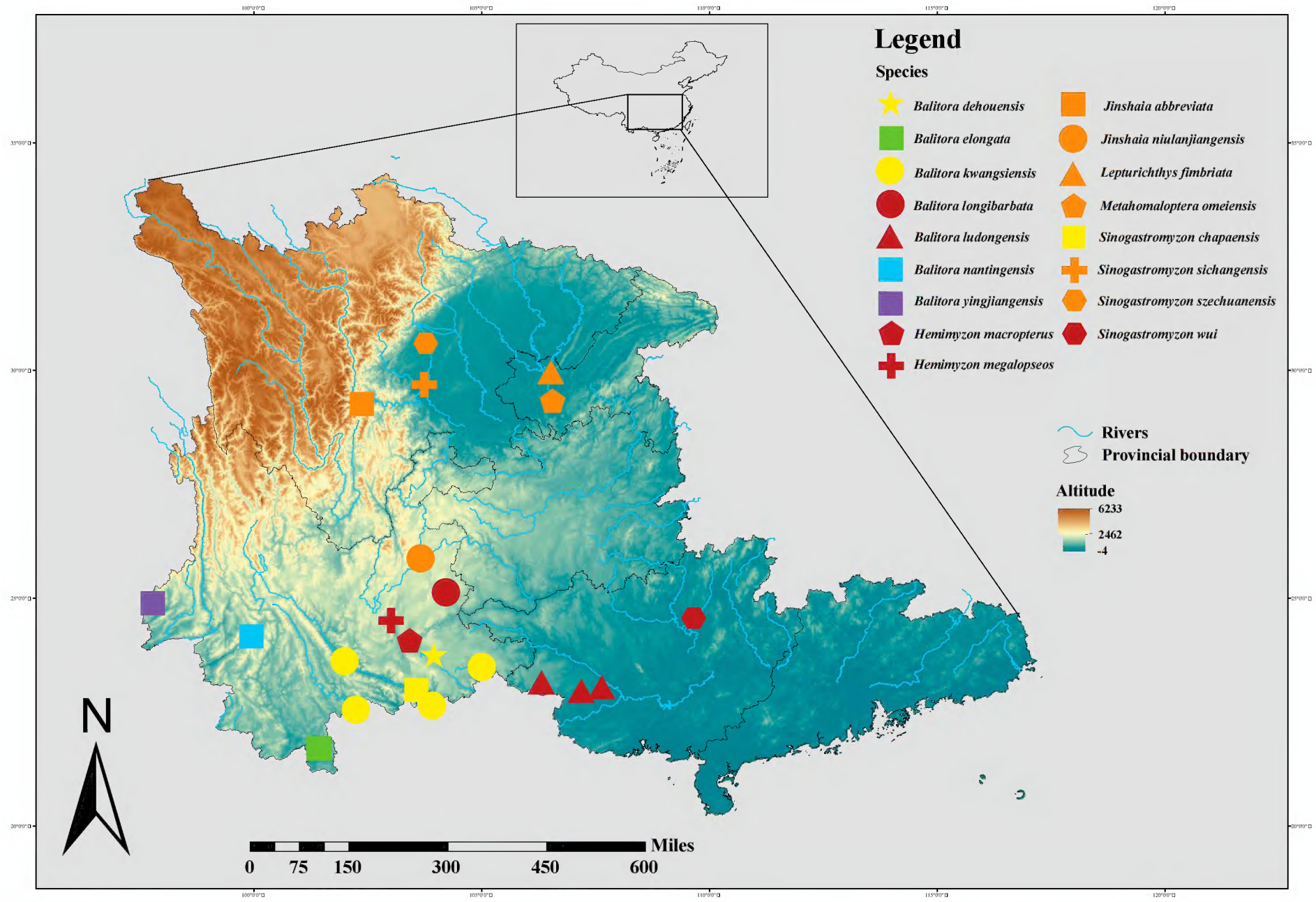

Figure 1. Map exhibiting sampling sites of 17 balitorid species in this study. Different colors represent different River drainage (Red: Pearl River; Yellow: Red River; Orange: Yangtze River; Green: Mekong River; Blue: Salween River; Purple: Irrawaddy River).

recombination activating gene 1 (RAG1), interphotoreceptor retinoid binding protein (IRBP), and early growth response protein 2B (EGR2B) of selected individuals (n = 26) were amplified and sequenced adopting the Protocols of DNA extraction and PCR amplification of Wu et al. (2024). Purification and sequencing in both forward and reverse directions were undertaken at Sangon Biotech (Shanghai, China) Co., Ltd.

The sequencing results were manually assembled using SeqMan II, and other sequences, especially those species not distributed in China, were acquired from the NCBI database. Newly generated sequences are deposited in GenBank under the accession numbers given in Table 1. A total of 52 Cyt *b*, 54 *CO*I, 43 RAG1, 37 IRBP and 37 EGR2B gene fragments were included in the phylogenetic analysis. Despite the incompleteness of molecular markers from GenBank in certain taxon, these sequences are included in the phylogeny to maximize the coverage of the phylogeny and provide a more comprehensive reconstruction. Sequences of each gene were aligned and manually examined separately in AliView (Larsson 2014) to ensure the correct reading frame. Alignments were concatenated using Phyx v.1.1 (Brown et al. 2017) to generate the final supermatix for phylogeny. Two methods were used to construct the phylogenetic tree for the concatenated dataset of two genes: maximum likelihood (ML) and Bayesian inference (BI). *Beaufortia szechuanensis* was included as an outgroup. ModelFinder (Kalyaanamoorthy et al. 2017) was used to select the best-fit model using Bayesian information criterion (BIC). All operations of ML and BI were done in PhyloSuite v1.2.2 (Zhang et al. 2020). Node support was determined by setting 20000 bootstrap (BS) replicates in ML and 20 million generations of Markov chains, sampling every 2,000 generations to yield 10,000 trees in BI. Tree is visualized in FigTree 1.4.4 (Rambaut 2018) and iTOL (https://itol.embl.de/).

Interspecific pairwise genetic distances of *B. dehouensis* with 11 other *Balitora* species included in the phylogeny are estimated based on Cyt *b* gene using MEGA11 (Tamura et al. 2021). based on the Kimura 2-parameter (K2P) model (Kimura 1980) with transitions + transversions substitutions, uniform rates, pairwise deletion and selecting all codon positions.

Results

Phylogenetic analysis

A total of 39 taxa and 57 individuals were included in the phylogeny (Fig. 2). The complete supermatrix comprised 4903 aligned sites (Cyt *b*: 1171 bp; *CO*I: 633 bp; RAG1:1466 bp; IRBP: 850 bp; EGR2B: 783 bp).

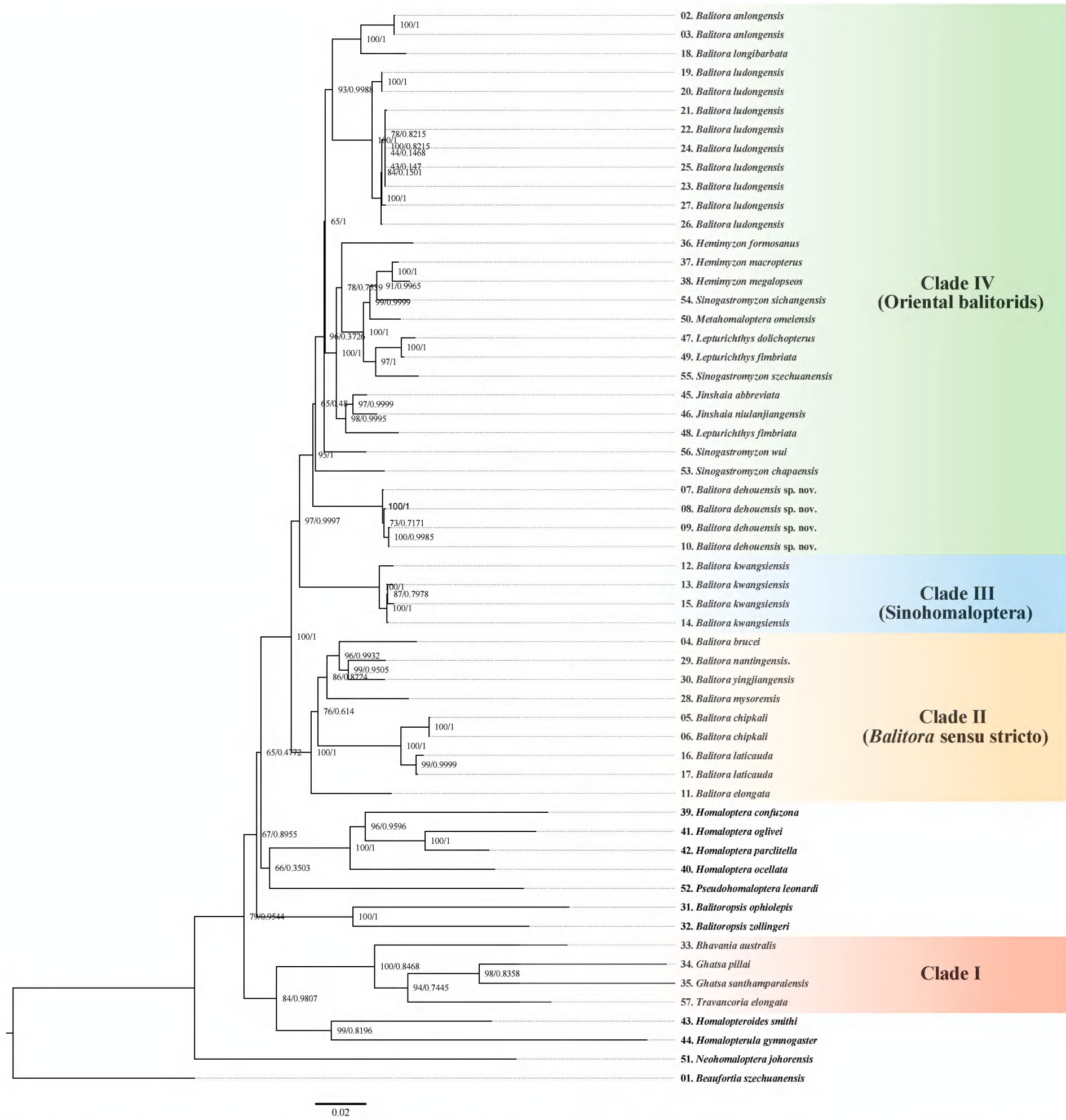

Figure 2. Phylogenetic tree of Balitoridae based on mitochondrial Cyt *b* and *CO*I gene as well as nuclear recombination activating gene 1 (RAG1), interphotoreceptor retinoid binding protein (IRBP), and early growth response protein 2B (EGR2B). The scale represents 0.02 nucleotide substitution at each site. numbers beside nodes are ultrafast bootstrap (UFB) supports from maximum likelihood (ML) analyses/Bayesian posterior probabilities (BPP) from Bayesian inference (BI) analyses.

Both phylogenetic methods (ML and BI) recovered highly consistent topology. *Balitora dehouensis* sp. nov. formed a well-supported monophylum. Phylogeny supported four major monophyletic clades in Balitoridae: Clade I consists of three genera endemic to the Western Ghats of India (*Bhavania*, *Ghatsa*, *Travancoria*); Clade II (*Balitora* sensu stricto) consists of all *Balitora* species from rivers to the west of the Red River, including the type species, *B. brucei*; Clade III (*Sinohomaloptera*) consists solely of *B. kwangsiensis*, the type species of genus *Sinohomaloptera* (currently synonym of *Balitora*); Clade IV (Oriental balitorids) consists of all members of Balitoridae distributed in the Red River, Pearl River, Yangtze River as well as Taiwan and Hainan Island except *B. kwangsiensis*, including *Balitora dehouensis* sp. nov. (Fig. 2). The smallest interspecific genetic distance (*p*-distance) between *B. dehouensis* and 11 other *Balitora* species ranges from 9.01% (in *B. ludongensis*) to 12.11% (in *B. chipkali*), significantly greater than maximum intraspecific *p*-distance of *B. dehouensis* (0.11%) (Table 3).

Systematics

Family Balitoridae Swanson, 1839

Type Genus: *Balitora* Gray, 1830.

Genus *Balitora* Gray, 1830

***Balitora dehouensis* Lei, Pu & Yang, 2025, sp. nov.**
https://zoobank.org/D710D8CC-2F4F-4154-A250-96DFF6DEE51A

Holotype. PXR20241123001, 61.1 mm SL; outlet of Lengfeng Cave, Dehou River, a tributary of the Lujiang River in Tieze Village, Dehou Town, Wenshan Zhuang and Miao Autonomous Prefecture, Yunnan Province, China (23.515678°N, 103.845043°E). Collected by Xin-Rui Pu, 24.XI.2024.

Paratypes. PXR20241123002-005(4), 44.5–29.0 mm SL; other data same as holotype. YHF20230925001-012 (12), 58.4–28.6 mm SL; Subterranean stretch of Dehou River, a tributary of the Lujiang River in Lengfeng Cave, Tieze Village, Dehou Town, Wenshan Zhuang and Miao Autonomous Prefecture, Yunnan Province, China. Collected by Hong-Fu Yang, 25.X.2023.

Diagnosis. A medium-sized balitorid with separated pelvic fins and two simple pelvic fin rays. Paired fins with no dark markings. Arched mouth with both jaws covered by a horny sheath; rostral flap divided into three lobes, separated by long rostral barbels; both lips with one row of indistinct papillae; two pairs of prominent maxillary barbels at corners of mouth, both longer than eye diameter. Oblique caudal-fin base, upper end significantly longer than lower end (Figs 8, 9). The upper lobe of caudal fin longer than lower.

Description. Morphological comparison of *B. dehouensis* with two other known troglobitic members of *Balitora* as well as their only congener possessing two pairs of long maxillary barbels, Namely *B. anlongensis*, *B. longibarbata* and *B. ludongensis* are demonstrated in Table 2. See Fig. 3 for a general profile of body. Body elongated, rounded laterally and flattened ventrally, posterior portion gradually compressed from dorsal fin to caudal-fin base, With the highest point of body at dorsal-fin origin. Body covered in small scales, lateral-line scales 74–78. Each scale with a prominent longitudinal keel along center. Lateral-line scales with two additional smaller keels along posterior edge, above and below principal longitudinal keel.

Head blunt and depressed, dorsum of head densely covered with tiny tubercles. Head length greater than head width and head width much greater than head depth. Eyes small, 2.31–1.05% SL; situated dorsally, slightly posterior to the midpoint of head, not visible from ventral view. Interorbital space wide and flat.

Mouth small, arched shaped, inferior, relatively shallow preoral groove present between rostral cap and upper lip, extending across corners of mouth. Rostral cape around upper lip and divided into three lobes by rostral barbels, the median one the largest, slightly curved. Two pairs of rostral barbels, both longer than eye diameter, outer one slightly longer than the inner one. Two pairs of long maxillary barbels, both exceeding eye diameter, outer one slightly longer than the inner one, situated at corner of mouth. Upper and lower jaws covered by a horny sheath. Upper and lower lips with a single row of large, indistinct papillae. Lower jaw with radiate ridges on surface. Two longitudinal fleshy ridges on mid-chin (Fig. 4). Gill opening large, extending to the pectoral fin origin on the ventral surface.

Dorsal fin rays i, 8, pectoral fin rays xi, 12, pelvic fin rays ii, 8, anal fin rays i, 5, and Principal caudal fin rays 7+8. Dorsal fin origin slightly anterior to pelvic-fin origin and nearer to tip of snout than to caudal fin base. Pectoral fins large and horizontally placed, posterior margin rounded. Tip of the pectoral fin not reaching pelvic fin origin. Pelvic fins short, not reaching or just reaching anus, posterior margin straight. Pelvic fin origin closer to snout tip than caudal fin base and closer to anal fin origin than snout tip. Pelvic fin not reaching anus. Anus situated approximately 2/3 distance from posterior end of the pelvic-fin base to the anal fin origin. Anal fin short, origin close to the anus and far from the caudal fin base, tips of which not reaching caudal fin base when extended backwards. Caudal-fin base oblique, upper end significantly longer than lower end. Caudal fin deeply forked, upper lobe longer than lower lobe. Uppermost and lowermost three or four principal caudal rays without interradial membranes and tightly associated. Caudal peduncle slender, length of which 4.82–3.37 times of depth.

Coloration. In living specimens: a comparison of live coloration of epigean and hypogean individuals of *B. dehouensis* is illustrated in Fig. 5.

In specimens from subterranean water bodies, body uniformly creamy yellow. Dorsum of head yellowish, covered with white tubercles. Dorsum of body with obscure dark blotches situated longitudinally in dorsal profile. Sides of body with scattered dark spots on scales. Dorsal fin rays golden, interradial membranes hyaline. pectoral and pelvic fin bases with dark blotches. Pectoral and pelvic fin rays golden, interradial membranes hyaline. Anal fin hyalin. Caudal-fin base with a rectangular dark blotch. Uppermost and lowermost caudal fin rays light brown, other rays golden. Interradial membranes hyaline. (Fig. 5).

In specimens collected from epigean waters, dorsal and lateral sides of the body greyish brown, creamy ventrally. Dorsum of head dark grey, covered with white tubercles. Medium of body with 8 saddle shaped dark blotches situated longitudinally in the dorsal profile. Sides of body uniformly dark grey. Dorsal fin rays dark grey, interradial membranes hyaline. Pectoral and pelvic fin bases brown with dark blotches from dorsal view. Pectoral and pelvic fin rays dark grey with

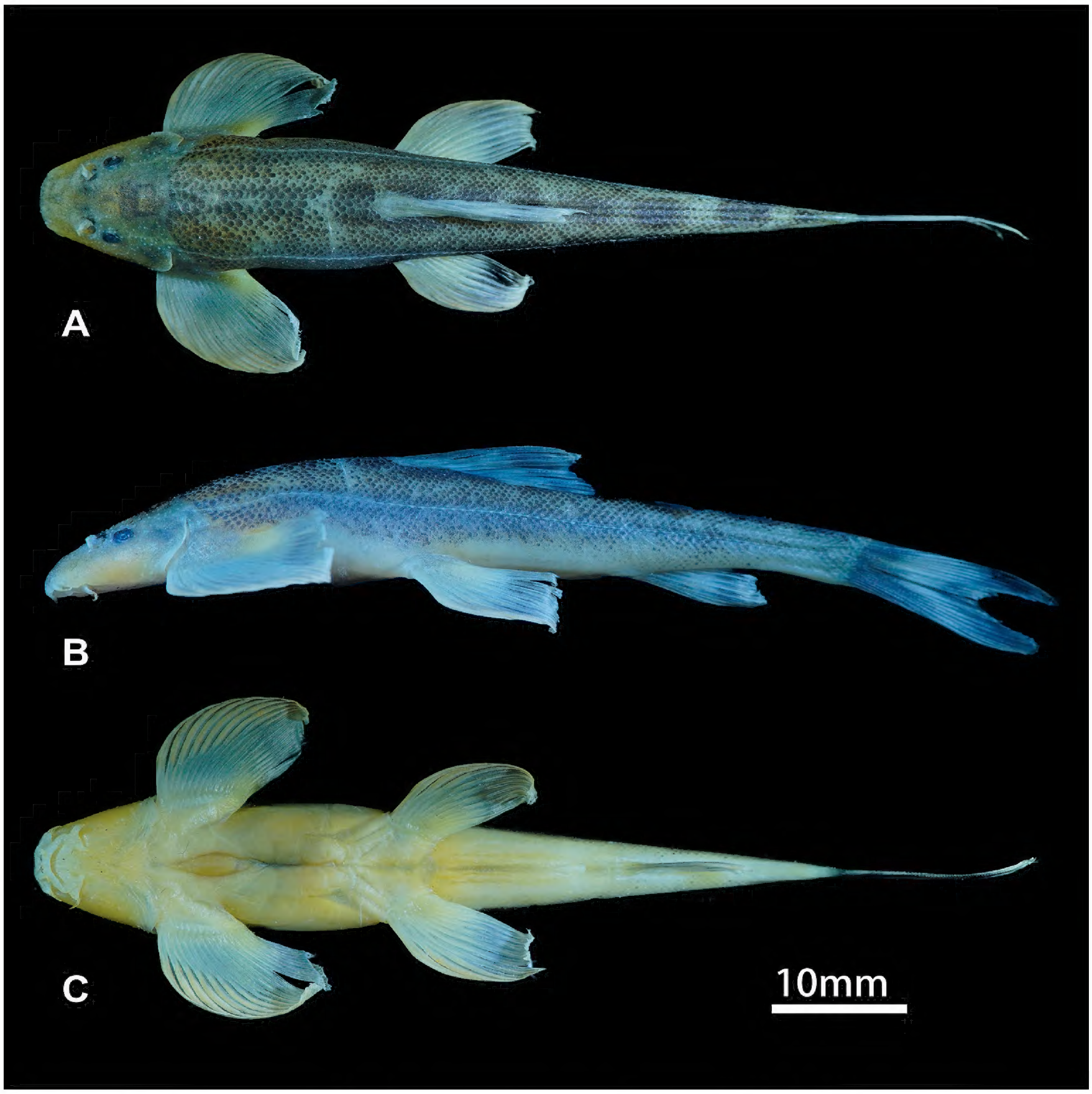

Figure 3. Morphological characteristics of *Balitora dehouensis* sp. nov. (Holotype, PXR20241123001); coloration in preservation. **A.** Dorsal view; **B.** Lateral view; **C.** Ventral view.

Figure 4. Oral morphology of *Balitora dehouensis* sp. nov.

no markings, interradial membranes hyaline. Anal fin hyalin. Caudal-fin base with a rectangular dark blotch. Caudal fin greyish with a black bar, closer to margin of fin than to caudal-fin base. Uppermost and lowermost fin rays dark grey. Interradial membranes hyaline. (Figs 5, 6).

In preserved specimens: coloration turned lighter in preservation, body background colour light grey to creamy white laterally and creamy-yellowish ventrally. Scales with scattered black spots Pigments on fins fainted.

Distribution and ecology. This species is presently only known from the outlet and subterranean river of Lengfeng Cave, a stretch of Dehou River (Fig. 7). This species inhabits torrential stretches of river with clear, well-oxygenated water as well as boulder and gravel substrate. Enlarged and flattened paired fins

Table 2. Morphometric comparison of *Balitora dehouensis* sp. nov and congener possessing two pairs of long maxillary barbels, i.e., *B. anlongensis*, *B. longibarbata* and *B. ludongensis*.

Characteristics	*B. dehouensis* sp. nov. (n = 17)				*B. ludongensis* (n = 9)			*B. anlongensis* (Luo et al. 2023)			*B. longibarbata* (n = 5)		
	Holotype	Range	Mean	S.D.	Range	Mean	S.D.	Range	Mean	S.D.	Range	Mean	S.D.
Dorsal-fin rays	III + 8½	III + 8½	III + 8½	/	III + 8½	III + 8½	/	III + 8½	III + 8½	/	III + 8½	III + 8½	/
Pectoral-fin rays	IX + 11½	IX + 11½	IX + 11½	/	VIII + 12	VIII + 12	/	VIII + 11	VIII + 11	/	VIII–X + 11–14	IX + 12	/
Pelvic-fin rays	II + 8½	II + 8½	II + 8½	/	II + 9	II + 9	/	II + 9	II + 9	/	II + 9–11	II + 9	/
Anal-fin rays	III + 5½	III + 5½	III + 5½	/	III + 5½	III + 5½	/	III + 5½	III + 5½	/	II + 5½	II + 5½	/
Caudal-fin rays	17	17	17	/	17	17	/	17	17	/	17	17	/
Lateral-line pore/ scales	77	78–74	76	/	72–68	70	/	68–66	67	/	76–74	75	/
Total length	76.15	76.15–38.36	50.35	/	77.52–47.73	63.03	/	60.40–47.90	55.90	/	91.08–66.02	81.04	/
Standard length (SD mm)	61.06	61.06–28.60	39.87	/	63.20–37.77	49.95	/	48.20–39.80	44.60	/	74.13–53.12	65.57	/
Head length	12.13	12.13–4.80	7.52	/	13.08–7.75	10.29	/	10.60–8.40	9.90	/	15.58–10.19	13.46	/
Caudal peduncle length/depth	3.78	4.82–3.37	3.96	0.167	2.73–2.05	2.33	0.129	3.39–2.70	3.04	/	4.42–3.39	3.80	0.422
Eyes parallel to head width/head width	0.86	0.87–0.72	0.81	0.051	0.96–0.82	0.88	0.050	/	/	/	0.99–0.83	0.90	0.066
Upper caudal lobe length/lower caudal lobe length	1.05	1.16–1.00	1.06	0.051	0.99–0.89	0.96	0.048	/	/	/	1.00–0.80	0.89	0.073
In percentage of SL													
Head length	19.87	24.34–18.36	20.29	0.016	21.86–19.32	20.58	0.007	23.71–20.54	22.16	0.009	21.02–19.18	20.47	0.007
Body depth	14.69	16.80–12.31	13.58	0.009	19.14–12.20	15.03	0.025	13.21–10.86	11.85	0.007	19.27–14.76	16.67	0.017
Body width	16.80	16.80–11.59	14.50	0.014	20.96–13.10	16.29	0.023	13.68–11.63	12.77	0.006	22.55–16.89	19.66	0.021
Caudal peduncle depth	5.56	5.80–5.18	5.46	0.002	8.57–6.75	7.69	0.007	7.31–5.78	6.51	0.004	6.37–5.38	5.85	0.004
Caudal peduncle length	17.79	21.81–17.01	18.99	0.014	20.10–15.22	17.89	0.016	21.52–17.73	19.69	0.011	23.79–21.12	22.07	0.010
Dorsal fin length	24.80	26.00–18.81	22.70	0.024	24.53–18.29	20.88	0.018	24.11–21.80	22.86	0.007	22.50–20.17	21.67	0.010
Pectoral fin length	22.80	23.08–19.27	21.59	0.009	24.19–19.71	22.45	0.014	25.63–23.17	24.19	0.009	27.94–24.48	26.37	0.013
Pelvic fin length	19.95	21.42–15.96	17.97	0.017	22.47–17.50	19.66	0.017	22.65–20.05	21.25	0.007	23.00–22.03	22.58	0.003
Anal fin height	16.98	17.18–14.57	16.01	0.007	18.46–13.69	15.86	0.018	19.06–17.22	17.98	0.006	19.09–16.32	17.12	0.011
Dorsal fin base length	15.02	15.95–10.98	13.43	0.017	15.30–12.39	13.70	0.009	15.98–12.53	14.63	0.010	16.60–9.85	13.25	0.024
Predorsal length	45.25	45.25–34.76	39.06	0.025	47.32–41.26	44.34	0.020	47.53–45.28	46.26	0.007	48.21–43.03	45.45	0.019
Prepelvic length	43.55	51.42–35.27	43.93	0.034	49.18–43.75	46.32	0.020	48.65–44.97	46.82	0.012	46.93–42.45	45.18	0.017
Preanal length	69.00	83.77–67.40	72.13	0.039	77.80–73.45	74.81	0.013	74.87–71.70	73.28	0.010	77.08–70.09	73.80	0.030
Snout length	6.52	6.82–5.53	6.78	0.004	9.00–7.29	8.37	0.005	12.79–11.62	12.22	0.004	9.61–9.11	9.29	0.002
Eye diameter	1.85	2.31–1.05	1.45	0.003	3.28–2.03	2.53	0.004	2.72–1.74	2.18	0.003	3.39–1.87	2.68	0.006
Interorbital width	7.49	7.99–5.24	6.50	0.008	9.08–7.63	8.28	0.005	10.38–7.63	9.35	0.008	8.08–6.82	7.43	0.004
In percentage of HL													
Inner rostral barbel length	10.39	12.84–10.50	11.04	0.009	15.75–7.65	11.75	0.024	28.57–19.23	23.16	0.031	15.26–9.72	12.23	0.022
Outer rostral barbel length	16.32	19.61–15.32	17.11	0.014	21.44–15.39	18.59	0.019	22.22–17.14	19.11	0.017	15.21–12.07	13.99	0.012
Inner maxillary barbel length	10.47	12.85–10.16	11.01	0.008	14.19–7.23	11.01	0.023	24.24–13.59	18.6	0.037	12.26–7.75	10.16	0.016
Outer maxillary barbel length	16.32	19.61–15.32	17.11	0.015	19.95–15.83	17.57	0.014	14.29–8.49	10.78	0.017	15.60–10.41	13.28	0.025
Mouth width	28.69	29.41–26.41	27.96	0.008	30.06–21.82	27.29	0.024	43.62–34.95	38.47	0.025	31.84–17.69	23.46	0.050

enable it to resist the current and adhere to the rocky surface while feeding on algae and aquatic invertebrates. During the rainy season, subterranean water levels rise, creating a riparian environment at the outlet of Lengfeng Cave ideal for *B. dehouensis*, making it possible to be collected outside the cave. During the dry season, subterranean water levels fall and *B. dehouensis* retreats into the cave. It was initially discovered by locals on 10.I.2023.(private communication). Syntopic fish species observed at the same locality with *B. dehouensis* include *Anabarilius transmontana* (Xenocyprididae), *Discogobio antethoracalis*, *Sinocyclocheilus wenshanensis* (Cyprinidae), *Homatula wenshanensis*, *Triplophysa wenshanensis* (Nemacheilidae) and *Paralepidocephalus yui* (Cobitidae).

Etymology. The specific epithet "dehouensis" refers to the type locality:Tieze Village, Dehou Town, Wenshan Zhuang and Miao Autonomous Prefecture, Yunnan

Figure 5. Morphological characteristics of *Balitora dehouensis* sp. nov. (Paratype, PXR20241123004); coloration in life. **A.** Lateral view; **B.** Dorsal view; **C.** Ventral view.

Table 3. Uncorrected minimum *p*-distance between *Balitora dehouensis* sp. nov. and 11 *Balitora* species based on mitochondrial Cyt *b* gene. Maximum intraspecific *p*-distance are given in bold at top of the block of each species (" / " for species with only one individual included in the phylogeny).

	Balitora dehouensis* sp. nov.	***Balitora anlongensis***	***Balitora brucei***	***Balitora chipkali***	***Balitora elongata***	***Balitora kwangsiensis***	***Balitora laticauda***	***Balitora longibarbata***	***Balitora ludongensis***	***Balitora mysorensis***	***Balitora nantingensis***	***Balitora yingjiangensis***
Balitora dehouensis sp. nov.	**0.0011**											
Balitora anlongensis	0.1026	**0**										
Balitora brucei	0.0962	0.1113	/									
Balitora chipkali	0.1211	0.1183	0.1078	**0.0005**								
Balitora elongata	0.1199	0.1129	0.1075	0.1087	/							
Balitora kwangsiensis	0.1074	0.117	0.1162	0.1296	0.123	**0.0005**						
Balitora laticauda	0.1175	0.1161	0.0963	0.0294	0.1059	0.1252	**0.0063**					
Balitora longibarbata	0.1048	0.0699	0.1155	0.1246	0.1195	0.1245	0.126	/				
Balitora ludongensis	0.0901	0.0827	0.1094	0.1104	0.1113	0.0975	0.1138	0.094	**0.0177**			
Balitora mysorensis	0.1027	0.1092	0.085	0.1049	0.1021	0.1223	0.9931	0.1225	0.1102	/		
Balitora nantingensis	0.1001	0.1018	0.0781	0.0936	0.0965	0.1104	0.0895	0.1221	0.0904	0.083	/	
Balitora yingjiangensis	0.1051	0.1036	0.08	0.0963	0.0898	0.1122	0.0929	0.1134	0.103	0.0809	0.0554	/

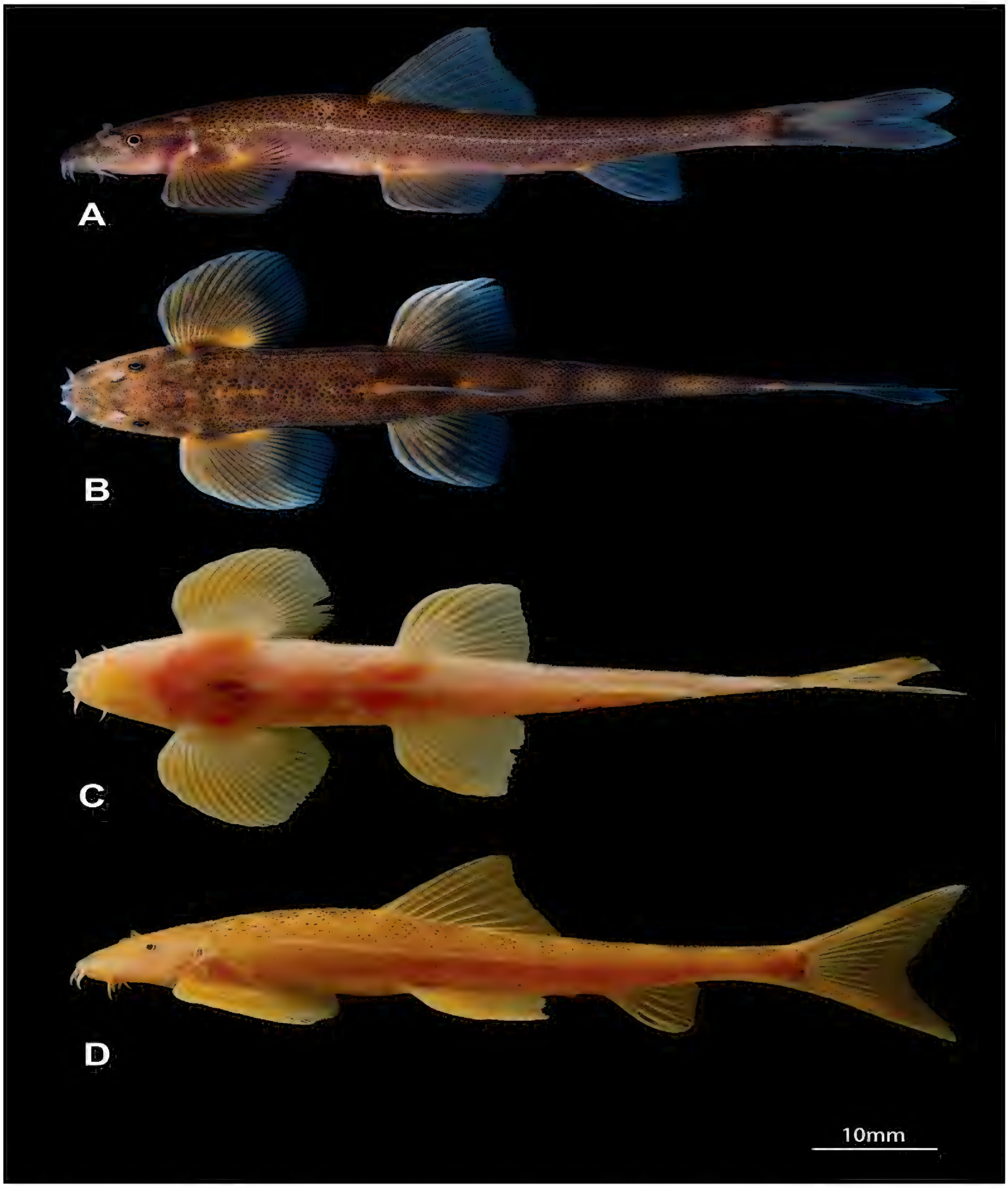

Figure 6. Comparison of colorations of hypogean and epigean individuals of *Balitora dehouensis* sp. nov. (PXR20241123001 & YHF20230925005). **A.** Lateral view of epigean individual (PXR20241123001); **B.** Dorsal view; **C.** Lateral view of hypogean individual (YHF20230925005); **D.** Dorsal view.

Province, China. Regarding the bizarre caudal-fin base of *B. dehouensis*, we propose the common English name "Dehou heterocercal stone loach" and the Chinese name "De Hou Yi Wei Pa Qiu (德厚异尾爬鳅)".

Remarks. *Balitora dehouensis* sp. nov. distinguished it from all other *Balitora* spp. from an oblique caudal-fin base (vs. vertical) and upper caudal fin lobe longer than lower (vs. equals to or shorter). *B. dehouensis* is further differentiated from *B. annamitica*, *B. brucei*, *B. burmanica*, *B. chipkali*, *B.eddsi*, *B. elongata*, *B. jalpalli*, *B. lancangjiangensis*, *B. laticauda*, *B. meridonalis*, *B. mysorensis* and *B. tchangi* in possession of two pairs of maxillary barbels (vs. one pair); from *B. kwangsiensis* as well as four Vietnamese species (*B. nigrocorpa*, *B. haithanhi*, *B. vanlani* and *B. vanlongi*) from both pairs of maxillary barbels longer than eye diameter (vs. both pairs of maxillary barbels not longer than eye diameter). *Balitora dehouensis* resembled *B. anlongensis*,

Figure 7. Type locality of *Balitora dehouensis*; photograph by Hong-Fu Yang.

B. longibarbata and *B. ludongensis* morphologically. It is differentiated from *B. anlongensis*, *B. longibarbata* and *B. ludongensis* by a shorter snout (snout length 6.82–5.53% SL vs. larger than 9% SL); it is further differentiated from *B. anlongensis* by a higher count of lateral line scales (78–74 vs. 68–66), shorter pectoral fins (pectoral fin length 23.08–19.27% SL vs. 25.63–23.17% SL) and smaller mouth (mouth width 29.41–26.41% HL vs. 43.62–34.95% HL); from *B. longibarbata* by narrower body (body width 16.80–11.59% SL vs. 22.55–16.89% SL), shorter pectoral fins (pectoral fin length 23.08–19.27% SL vs. 27.94–24.48% SL) and shorter pelvic fins (pelvic fin length 21.42–15.96% SL vs. 23.00–22.03% SL); from *B. ludongensis* by higher count of lateral line scales (78–74 vs. 72–68), slender caudal peduncle (length of caudal peduncle 4.82–3.37 times of depth vs. 2.73–2.05) and shallower caudal peduncle (depth of caudal peduncle 5.80–5.18% SL vs. 8.57–6.75% SL).

Discussion

The discovery of new troglobitic balitorid brings new insights into cave adaptation

Significant morphological similarity occurred between *Balitora dehouensis* sp. nov. and three *Balitora* species from the upper Pearl River, *B. anlongensis*, *B. longibarbata* and *B. ludongensis* in a similar oral morphology, characterized by two pairs of long maxillary barbels, long rostral barbels and one row of obscure papillae around lips (Fig. 4). It further resembled *B. anlongensis* and *B. ludongensis* in small eyes, lack of dark blotches on sides of body and paired fins, typical features of troglobite (Romero and Paulson 2001). Among these species, *B. anlongensis* was reported to be a troglobitic species in the original description (Luo et al. 2023), while *B. ludongensis* was collected from a cave in Longan County, Nanning City, Guangxi Zhuang Autonomous Region, China during sample collection procedure of this research, identity of these specimens were confirmed through morphological and phylogenetic analyses (Figs 2, 10). Phylogeny of this study supports *B. anlongensis*, *B. longibarbata* and *B. ludongensis* to be closely related sister species, yet *Balitora dehouensis* sp. nov. is neither closely related to them nor to any other balitorid. Although both the three species from the Pearl River and *B. dehouensis* might not genuinely be *Balitora* species according to the present phylogeny and/or multiple genera need to be established to reflect the natural groups, we decided not to make the change at this stage given the incompleteness and limited number of molecular markers used in this study. Thus, *B. dehouensis* is assigned to *Balitora* in this study based predominantly on morphology to avoid further contributions to the chaotic generic classification of Balitoridae.

Among all other balitorids with deeply forked caudal fins, the lower caudal fin lobe is either equal to or longer than the upper lobe (Chen 1980; Kottelat 1988a, Kottelat and Chu 1988), a feature common in rheophilic benthic freshwater fishes (Lujan and Conway 2015). However, in *Balitora*, the upper lobe is longer than the lower (Figs 8, 9). Hora (1936) reported that similar differences in caudal fin shape were observed in Nemacheilidae and assumed that such differentiation reflected adaptations to different habitats, as nemacheilids with a longer upper caudal lobe are found from lakes, with a slower flow rate, whereas those with longer lower caudal lobe are common in torrential rivers. A dramatic seasonal change of subterranean water level was observed at the type locality of *B. dehouensis*, resulting in a highly variable river terrain. Although *B. dehouensis* resembles other balitorids in the preference of riparian habitat, they could be trapped in deep, slow-flowing pools while the subterranean water level falls. In conclusion, the uniquely derived caudal fin shape of *B. dehouensis* might be adaptations for this constantly changing environment. The discovery of *B. dehouensis* addressed the importance of caudal fin shape as a troglobitic characteristic and provided new insights into the adaptation of troglomorphic members of highly rheophilic taxa.

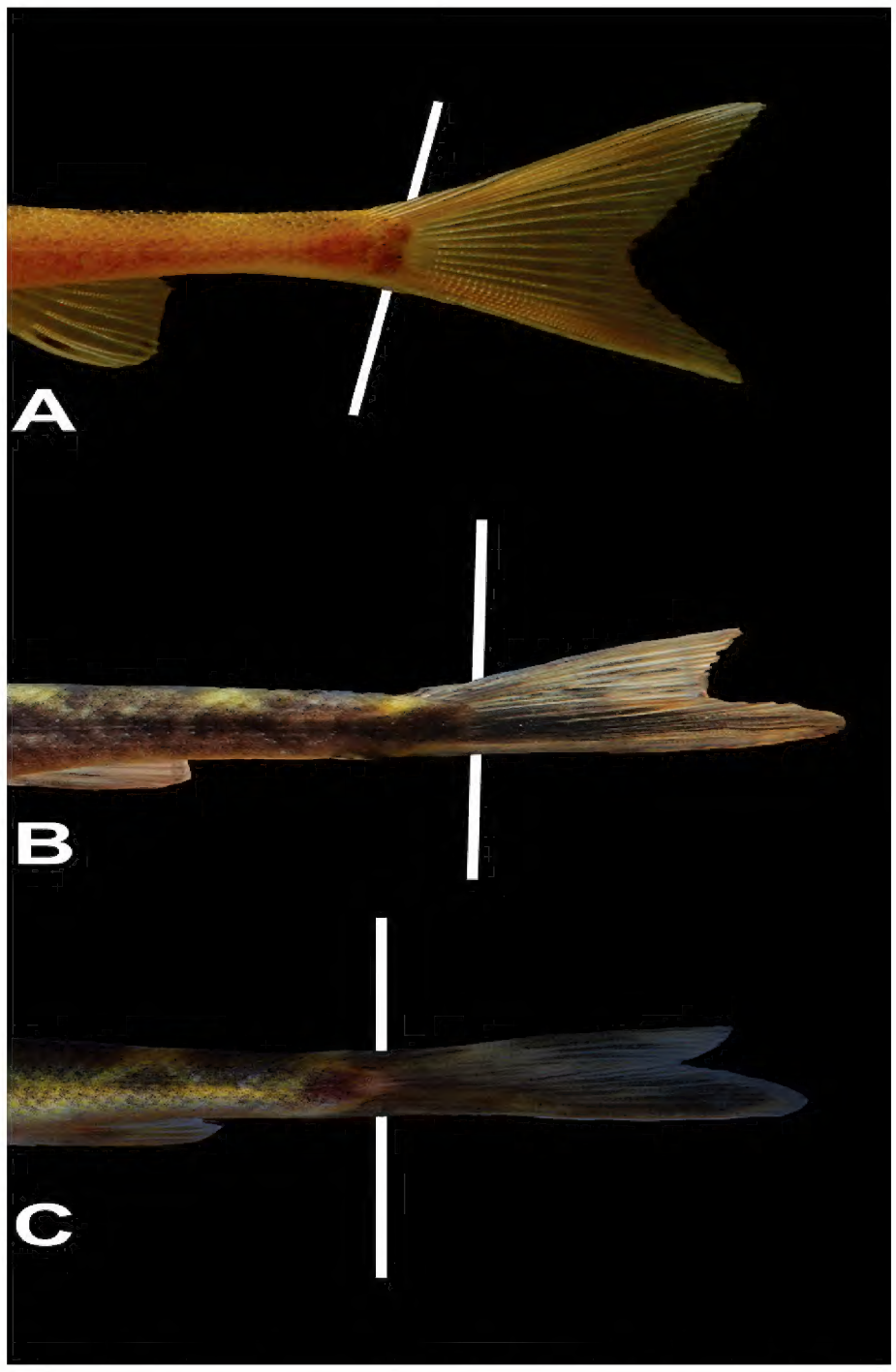

Figure 8. Comparison of caudal fin base of *Balitora dehouensis* sp. nov. and other Balitorids in life. **A.** *Balitora dehouensis*; **B.** *Balitora yingjiangensis*; **C.** *Balitora kwangsiensis*.

Further research on Balitoridae taxonomy prioritizes dataset expansion

Various attempts to elucidate taxonomic relationships within Balitoridae through phylogenetic analyses have been conducted (Liu et al. 2012a; Randall and Page 2015; Randall and Riggs 2015; Randall et al. 2023; Kumkar et al. 2016; Keskar et al. 2018; Tao et al. 2019; Shao et al. 2020; Sidharthan et al. 2021; Luo et al. 2023), yet the majority of which were restricted to a limited selection of species. To date, a comprehensive phylogeny of Balitoridae is yet to come. In this study, we reconstructed the largest phylogeny of Balitoridae so far, covering 15 of 16 currently valid balitorid genera. The aforementioned phylogenetic placements are in congruence of previous research (Tao et al. 2019; Shao et al. 2020; Sidharthan et al. 2021; Luo et al. 2023).

However, the dataset in this study is incomplete and limited to five molecular markers. These limitations might lead to insufficient credibility of the current phylogeny as primary accordance for assigning intergeneric relationships and subfamilial delineation.

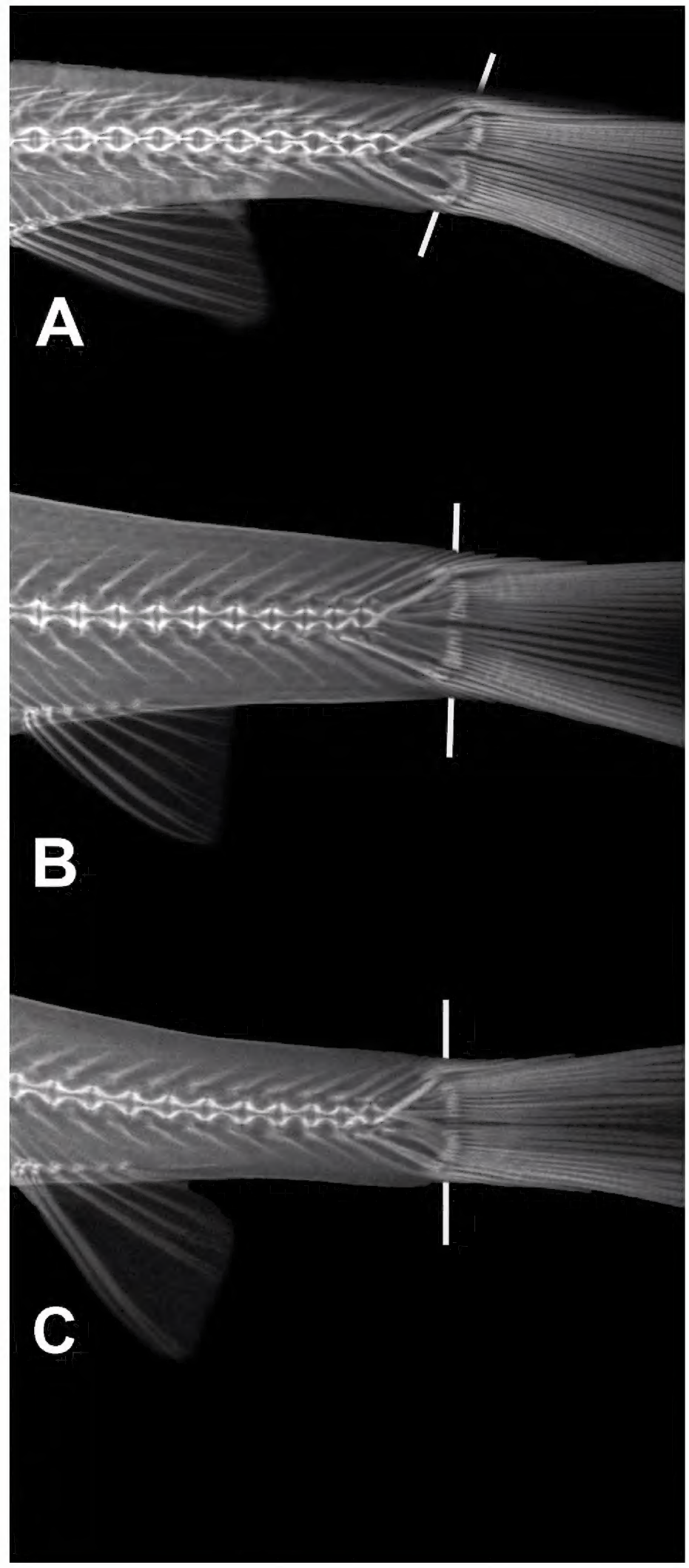

Figure 9. Comparison of caudal fin base of *Balitora dehouensis* sp. nov. and other Balitorids under X-ray. **A.** *Balitora dehouensis*; **B.** *Homaloptera confuzona*; **C.** *Balitora ludongensis*

We did not propose any systematics assignment to the current generic taxonomy regarding such defects. An increase in molecular sampling density, standardization of appropriate molecular markers, expansion of taxon sampling, as well as exploration of reliable morphological features that coheres with the phylogeny could be the priorities of future research on Balitoridae taxonomy.

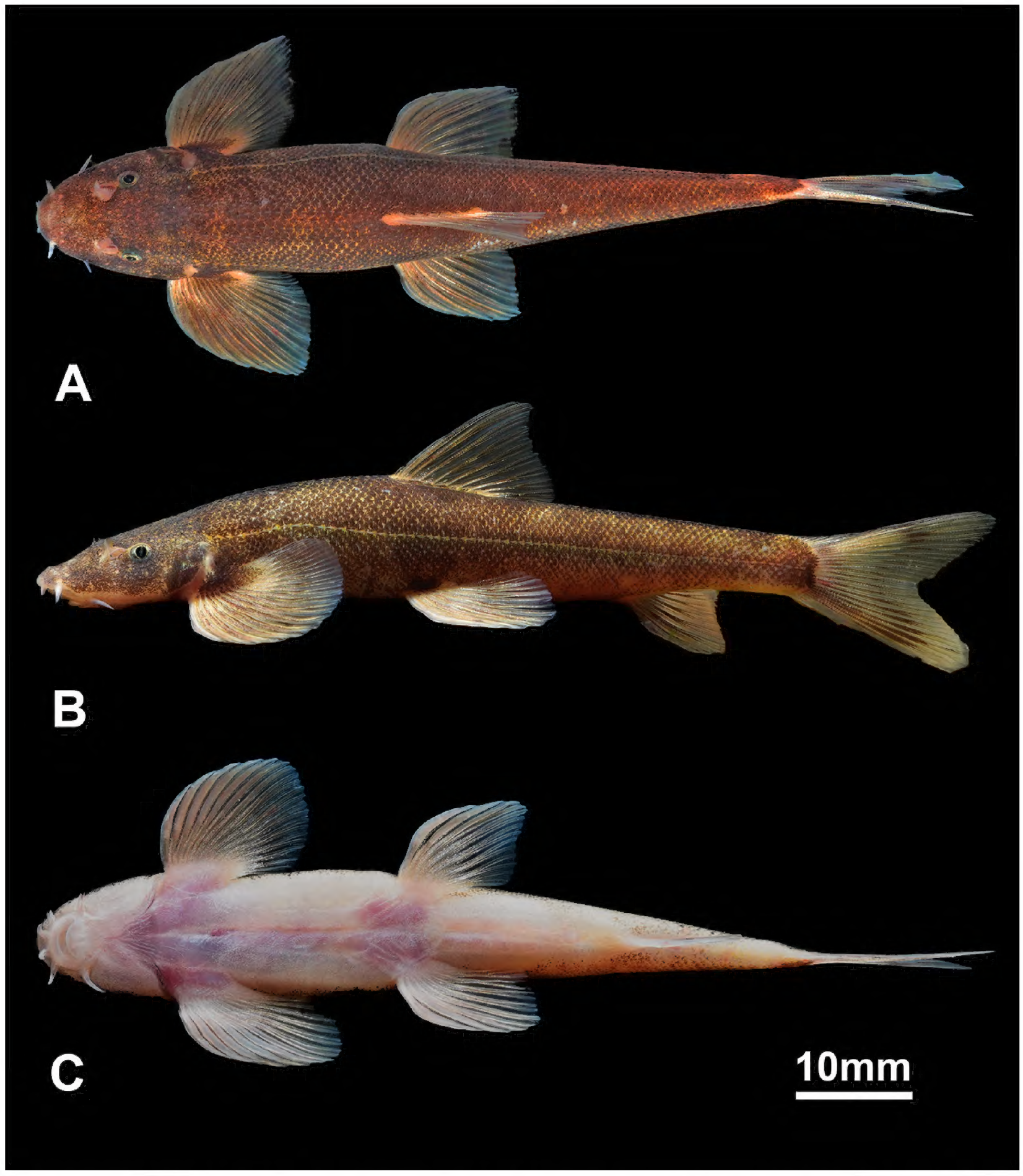

Figure 10. Morphological characteristics of hypogean *Balitora ludongensis* (20250105004); coloration in life. **A.** Dorsal view; **B.** Lateral view; **C.** Ventral view.

Acknowledgements

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